mess of hot beans, washed down with unpalatable, but also hot, ersatz coffee put a new light on things.

The next morning, with little ado, we packed and started on the last lap of our trip. We were not only still intact, but we noted that our ranks had increased by the addition of a lone burro, which soon became the whipping-boy for the caravan.

After a night's stop at Tecolote (Pl. 8), we traveled on the next day to the upper slopes of Sierra Chinatú, within two hours of San Juan. The animals were, to put it mildly, completely fagged, so we made camp. Searching our meagre "kitchen" we came up with a handful of rice, along with a few scrawny potatoes and two eggs we had purchased from the Tarahumares. The eggs helped to thicken the greaseless stew which we gratefully consumed amid our thoughts.

Dr. Gentry and I got an early start the next day, Wednesday, October 21, and rode on into San Juan in search of some breakfast while the muleteers and Juan searched for a burro that had started back home during the night. With about fifteen pounds already shed from my frame and little twitches of hunger within, it is not at all strange that I recall those last two hours on the trail as the most fernless encountered during the entire trip.

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Multicellular and Branched Hairs on the

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Hairs are a common feature on the sporophyte of ferns and are usually present on young parts if not on the mature. Bower (1923) made a sharp distinction between simple hairs and multicellular scales as indicators of phylogeny. As might be expected, hairs are not as highly developed or as numerous on the gametophyte. It remains to be seen if the types and distribution of hairs will be of any assistance in questions of phylogeny.

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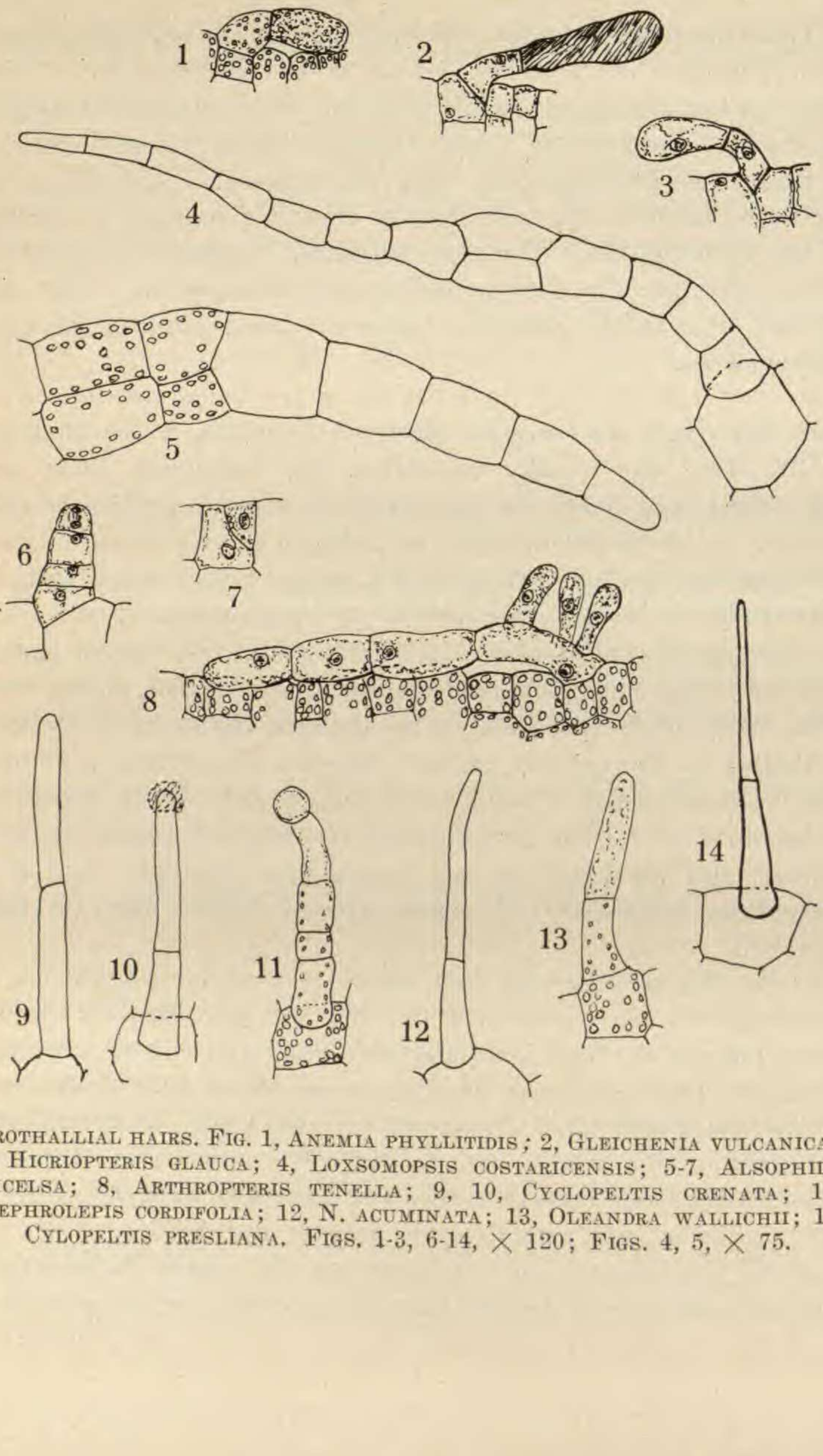
[1] This account is based on studies of cultures which have been maintained in connection with the investigations carried on in coöperation with Dr. Lenette R. Atkinson for the past ten years, and on my own earlier cultures.

There are many families, especially among the primitive ferns, in which hairs are entirely lacking on the gametophyte. They have not been found in the Marattiaceae, Osmundaceae, Hymenophyllaceae, Matoniaceae, Dipteridaceae, Plagiogyriaceae, Cheiropleuriaeceae, Dicksoniaceae, and Vittariaceae. (The Hymenophyllopsidaceae is the only family of which nothing is known of the gametophyte.) The most primitive families with gametophyte hairs are the Gleicheniaceae and Schizaeaceae; they are present, also, in the somewhat more advanced Cyatheaceae and Loxsomaceae.

In the Gleicheniaceae the hairs are never numerous, but have been described for several species (Campbell, 1908, Stokey, 1952). They are usually two-celled, less frequently three- or four-celled, and borne on the dorsal or ventral surface of the midrib. In the Gleicheniaceae, and also in the Cyatheaceae and Loxsomaceae, the hair arises from a special initial cell, a wedge-shaped cell on the anterior face of a young superficial cell near the apex of the thallus (*Figs. 6, 7*). Growth at this stage is rapid and the young hair soon projects above the surface, forms two cells, rarely more, and then curves towards the apex. A section of thallus of *Hicriopteris glauca* (Thunb.) Ching with a young hair is shown in *Fig. 3*, and an older hair of *Gleichenia vulcanica* Blume in *Fig. 2*. The terminal cell elongates, becomes slightly bulbous and filled with a heavily-staining substance, and the protoplasm disappears; the same process follows later in the basal cell.

In the Schizaeaceae the hair arises as a simple papilla on a marginal cell, less frequently on the surface (Bauke, 1878). When mature the hair is usually two-celled and curved towards the apex. The hair shown in *Fig. 1* was found on a thallus of *Anemia phyllitidis* (L.) Swartz only 46 days old. Hairs are not abundant in this family, and on *Lygodium palmatum* (Bernh.) Swartz they were found on only two prothalli (Rogers, 1923); they agreed in type with those of *Anemia* and *Mohria*.

In the Cyatheaceae and Loxsomaceae, the multicellular hairs arise not only from a special initial but are of a special scale-like

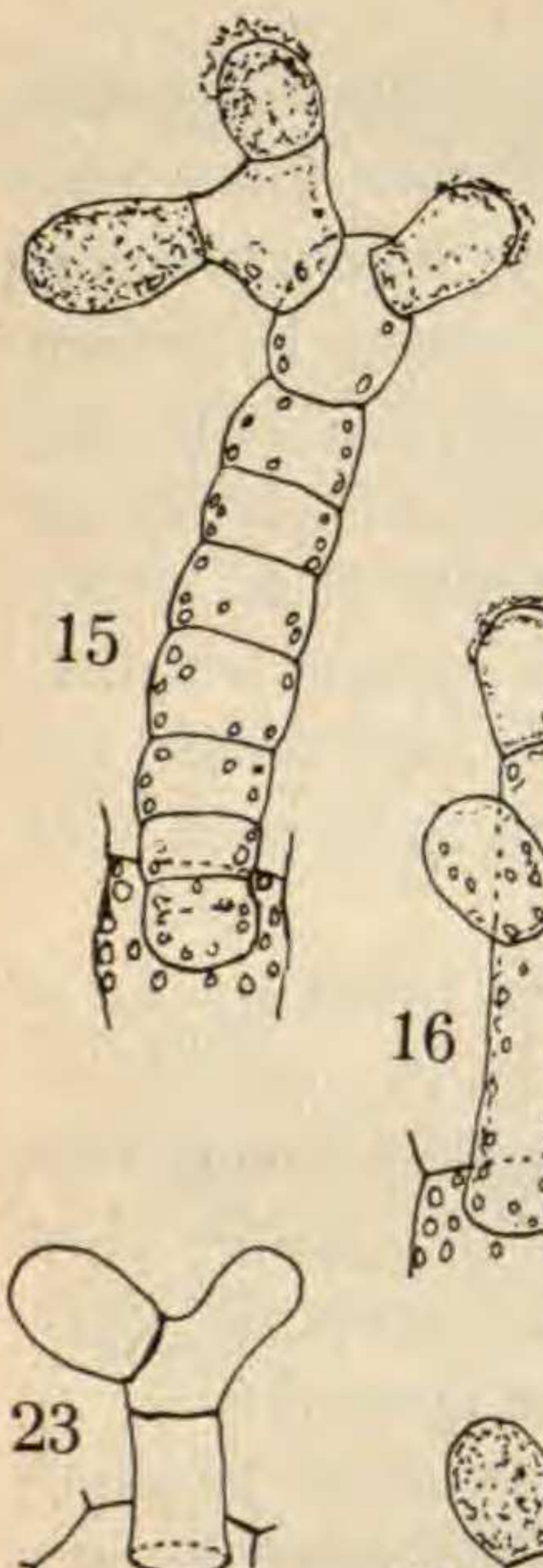


PROTHALLIAL HAIRS. FIG. 1, ANEMIA PHYLLITIDIS; 2, GLEICHENIA VULCANICA; 3, HICRIOPTERIS GLAUCA; 4, LOXSOMOPSIS COSTARICENSIS; 5-7, ALSOPHILA EXCELSA; 8, ARTHROPTERIS TENELLA; 9, 10, CYCLOPELTIS CRENATA; 11, NEPHROLEPIS CORDIFOLIA; 12, N. ACUMINATA; 13, OLEANDRA WALLICHII; 14, CYLOPELTIS PRESLIANA. FIGS. 1-3, 6-14, × 120; FIGS. 4, 5, × 75.

type (Bauke, 1876; Goebel, 1912; Stokey, 1930; Stokey & Atkinson, 1956). These hairs are one to several cells wide, many cells long, and usually have a tapering slender tip, as in *Loxsomopsis costaricensis* Christ (*Fig. 4*) and *Alsophila excelsa* R. Brown (*Cyathea Brownii* Domin) (*Fig. 5*), in which the hairs are often much longer. Bauke described them in his account of the Cyatheaceae as "Borsten." They arise, usually after archegonium production has begun, on or near the cushion on both dorsal and ventral surfaces, curving towards the notch and making a green brush-like growth large enough to be seen with the naked eye.

In the families formed in recent years by the breaking up of the old comprehensive family Polypodiaceae, hairs, unicellular, multicellular, and branched, are more abundant and varied than in the four families discussed. It is convenient to consider them on the basis of Copeland's classification (1947), with the addition of the Grammitidaceae which he recognized later (1951). It is in these higher families that the familiar type of papillate hair, unicellular and usually glandular, has developed in profusion. The multicellular hair, even when two-celled, is much less common and seldom present in abundance. A two-celled hair may properly be considered a multicellular hair; it seldom appears as a chance modification of a one-celled hair, and its variants are apt to be three- or four-celled.

In the Davalliaceae multicellular and even branched hairs are found occasionally. On the thallus of *Davallia denticulata* (Burm.) Mett. a few two-celled and branched hairs were found. On the gametophyte of *Oleandra* the abundant long unicellular hairs are often borne on extensions of marginal cells and suggest two-celled hairs; examples of true two-celled hairs were found in *O. wallichii* (Hook.) Presl (*Fig. 13*). In *Nephrolepis*, multicellular hairs were more abundant, especially on the thallus of *N. cordifolia* (L.) Presl, but less numerous and shorter on *N. acuminata* (Houtt.) Kuhn (*Fig. 12*). On *Humata heterophylla* (J. E. Smith) Desv., a marginal three-celled branched hair was found near the notch. On the thallus of *Arthropteris orientalis*



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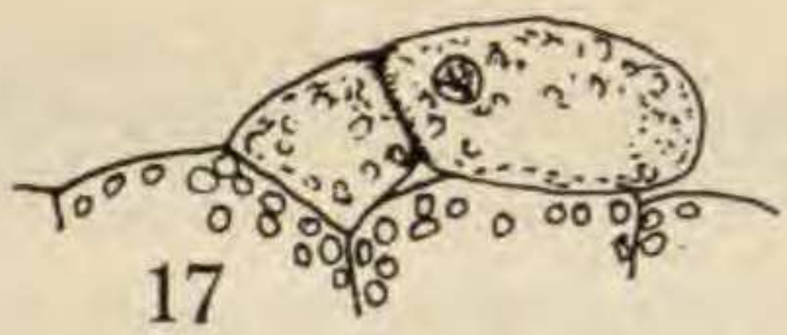

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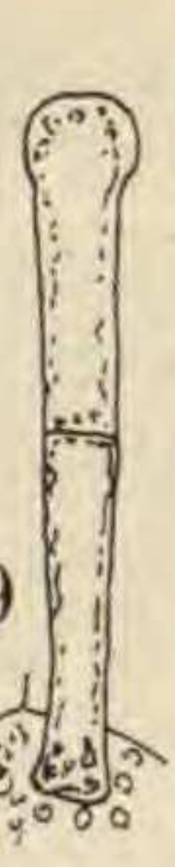

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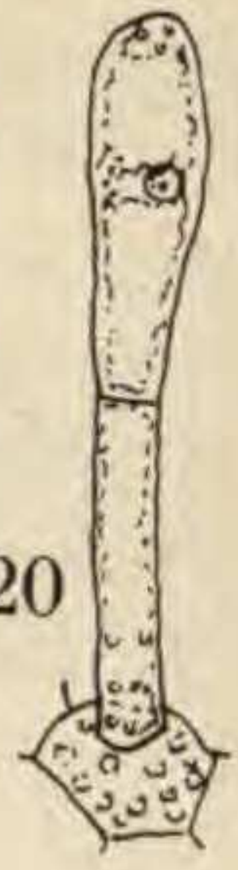

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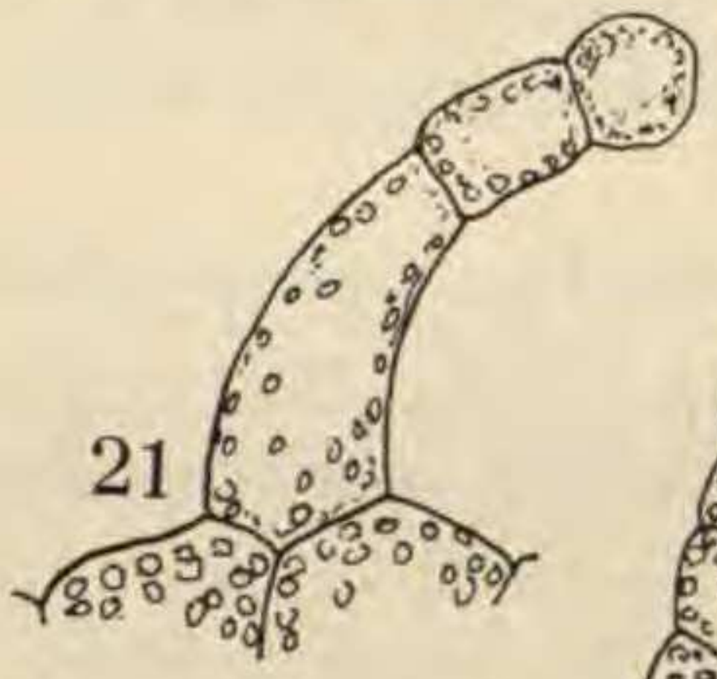

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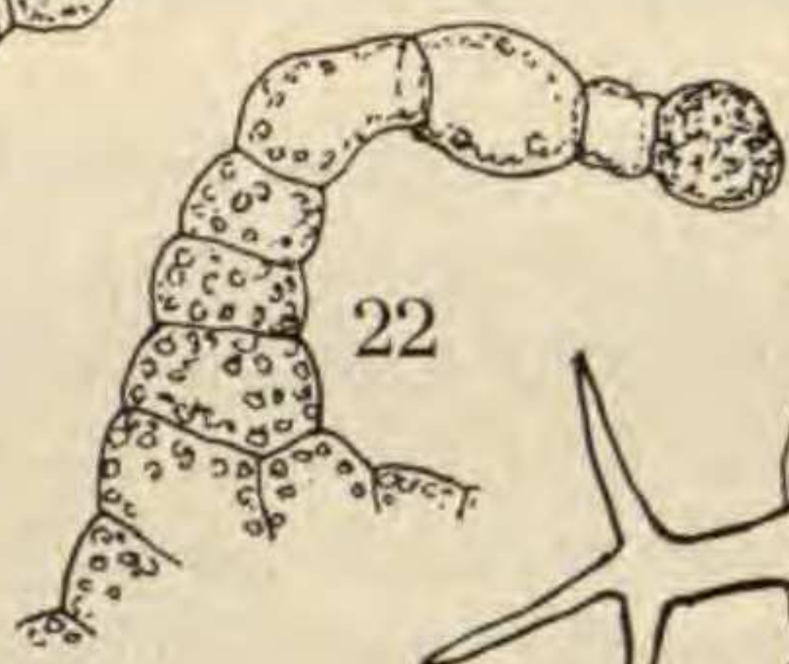

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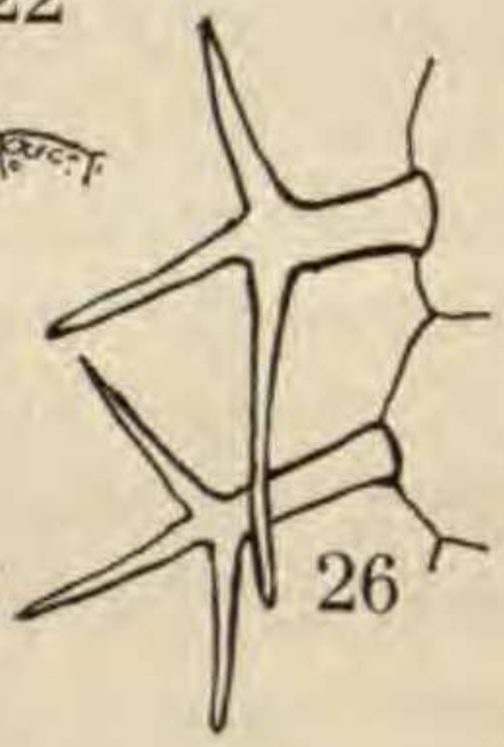

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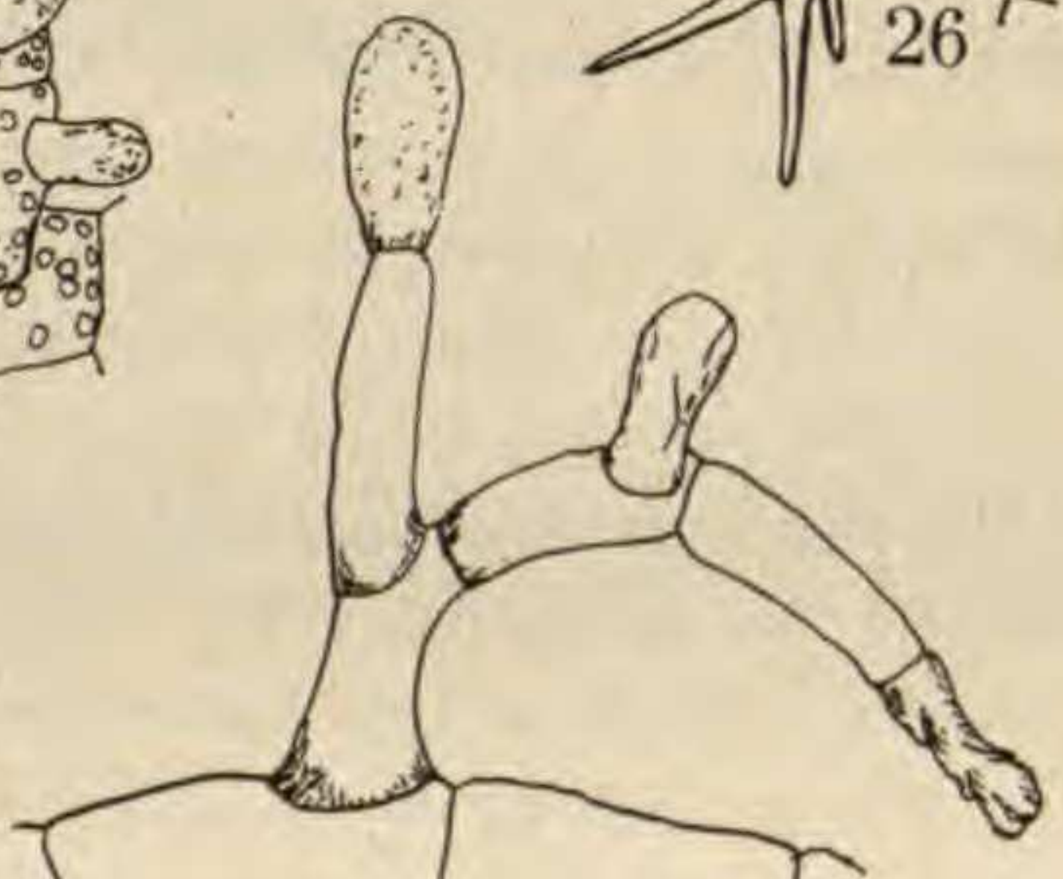

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PROTHALLIAL HAIRS. FIG. 15, PLATYCERIUM ALCICORNE; 16, P. GRANDE; 17, LOXOGRAMME PARKSII; 18, BOLBITIS QUOYANA; 19, 20, PLEUROSORUS RUTIFOLIUS; 21, 22, CETERACH OFFICINARUM; 23, PALTONIUM LANCEOLATUM; 24, PYRROSIA CHINENSIS; 25, PESSOPTERIS CRASSIFOLIA; 26, THELYPTERIS BIOLLEYI; 27, XIPHOPTERIS DELITESCENS; 28, CTENOPTERIS JUBIFORME; 29. C. ASPLENIFOLIA. ALL × 120.

(Gmel.) C. Chr. several examples of three-celled simple hairs were found on the ventral surface near the archegonia. On that of *A. macrocarpa* (Cordem.) C. Chr. there were three-celled simple hairs on the dorsal and ventral surfaces, and branched hairs with as many as six cells appressed to the ventral surface. *Arthropteris tenella* (Forst.) J. Smith had more hairs, all appressed to the margin and curved towards the apex; some were simple and others elaborately branched (*Fig. 8*).

In the large and diverse assemblage of the Aspidiaceae, it is not unusual to find species in which multicellular hairs are borne on the gametophyte. On the prothallus of *Cyclopeltis crenata* (Fée) C. Chr. two-celled hairs were found on the surface but more abundantly on the margin, often with a glandular tip which gave a reaction for wax with Sudan IV (*Figs. 9, 10*); a few branched hairs were found on the surface. The same type of two-celled hair was found in large numbers on the thallus of *C. presliana* (J. Smith) Copel. even two or three on a single marginal cell. On the thallus of *Bolbitus quoyana* when eight weeks old there appeared on the margin two-celled hairs curving towards the apex (*Fig. 18*); at three months they were present on the margin in a close growth of curved colorless hairs of two or three cells with the terminal sometimes inflated; a few of the hairs were branched. Later branched hairs appeared on the dorsal surface. On the prothallus of *Phanerophlebia caryotidea* (Wall.) Copel. and on that of *Rumohra aristata* (Forst.) Ching a few short two-celled hairs were found. *Pteridrys australis* Ching had a liberal development of branched hairs with four to eight cells on both dorsal and ventral surfaces of the midrib. Two-celled hairs are not uncommon on the surface and margin of the gametophyte of *Pleocnemia conjugata* (Blume) Presl; branched hairs are relatively rare. The five species of *Tectaria* in our cultures showed multicellular or branched hairs or both: *T. incisa* Cav., *T. decurrens* (Presl) Copel., *T. irregularis* (Presl) Copel., *T. griffithii* (Baker) C. Chr., from Nepal, and *T. subtriphylla* (H. & A.) Copel. The hairs were mostly on the surface, rarely on the margin, usually three-celled but sometimes

four- or five-celled. On a rather sparse culture of *Heterogonium pinnatum* similar branched hairs were found on several gametophytes. *Cyclosorus* is unusual in having acicular hairs on the gametophyte of several species usually one-celled but in the case of *C. parasiticus* occasionally two-celled (*Fig. 14*). *Thelypteris* (*Goniopteris*) *biolleyi* (Christ) Proctor has an unusual type of hair—branched stellate hairs similar to those found on the sporophyte, but there were no indications of apogamy. They appeared rather sparingly at three months on the ventral surface before archegonia had developed; they were present in great numbers on both margin and surface of cushion and wings when the cultures were nine months old, and archegonia were abundant (*Fig. 26*).

In the Aspleniaceae there is a considerable range in regard to hairs on the gametophyte, as was pointed out by Wagner (1953). A type of multicellular hair which ends in a gland was found on *Diellia* gametophytes, and also on those of *Ceterach dalhousiae* (Wagner, 1952); he found the same type on the thallus of *Asplenium leucostegioides* Baker (1953). The same type is present also on the prothallus of *C. officinarum* with considerable variation in length (*Figs. 21, 22*). It occurs also on the gametophyte of *A. flabelliforme* Cav., appearing when the prothalli are three to four months old, on the margin near the notch both before and after the production of archegonia. On some gametophytes of the same age and on some slightly older, apogamous sporophytic outgrowths associated with clathrate scales appeared. On the prothallus of *A. septentrionale* (L.) Hoffm. among the many long unicellular hairs there are occasionally two-celled and even branched hairs. The prothallus of a tetraploid *Phyllitis scolopendrium* var. *americana* Fernald (spores from a Michigan plant) when five months old had a considerable number of two- and occasionally three-celled hairs, straight or slightly curved, on both dorsal and ventral surfaces, as well as on the margin near the apex. There were only one-celled hairs in a culture of *Phyllitis scolopendrium*, presumably diploid, raised from spores collected in Mürren, Switzerland. The gametophyte

of *Pleurosorus rutifolius* (R. Brown) Fée when less than four months old bore a considerable number of long two-celled hairs among and in front of the archegonia (*Figs. 19, 20*).

The description and figures by Klein (1881) of the prothallus of *Polypodium heracleum* Kunze [*Drynariopsis heraclea* (Kunze) Ching] is the classic account of branched hairs on a fern gametophyte. Recent work indicates that the Polypodiaceae *sensu stricto* is the group in which branched hairs appear on the gametophyte of the largest number of species, although the range in type is not known to be as great as in some other groups. Multicellular simple hairs are not unusual in young cultures which later produce branched hairs. The most common type of branched hair is usually three-celled, such as that of *Paltonium lanceolatum* (L.) Presl (*Fig. 23*), and that of *Pyrrosia lingua* (Thunb.) Farw. (*Fig. 24*), with the four- or five-celled, as in *Pessopteris crassifolia* (L.) Underw. & Maxon (*Fig. 25*) less frequent. This type of hair is usually found on the surface, on or near the midrib and rarely on the margin.

There is much variation in the age of thallus at which branched hairs appear, but it is regularly later than that for simple unicellar hairs. *Pleopeltis hastata* (Thunb.) Moore began the production of branched hairs at 75 days; *Pessopteris* had branched hairs with seven cells at three months; *Pyrrosia lingua* had branched hairs with three to six cells at 10 weeks. In *Phlebodium aureum* (L.) J. Smith, *Belvisia spicata* (L.) Mirb., and *Campyloneuron phyllitidis* (L.) Presl branched hairs were late in developing with some variation in different sets of cultures. They appeared sparingly in a culture of *P. virginianum* L. at seven to nine months. They were found on the following species of *Polypodium* at varying times: *P. chnoodes* Spreng., *P. pectinatum* L., *P. plebejum* Schlecht. & Cham., *P. repens* Aubl., and *P. vexatum* D. C. Eaton. They appeared also on *Aglaomorpha meyeniana* Schott, *Microsorium scolopendria* (Burm.) Copel., and *M. punctatum* (L.) Copel.; in addition to branched hairs, which appeared at six months, they also bore clathrate scales. Nayar (1957) has reported branched hairs on the prothallus of

Drymoglossum piloselloides (L.) Presl. The large branched hairs on the thallus of *Platycerium* (Straszewski, 1915; Stokey & Atkinson, 1954) are similar to the branched hairs described for other members of the family except that they are unusually large and abundant; the stalk cells are green and the tips of the branches glandular (*Figs. 15, 16*).

In *Loxogramme*, a genus whose systematic position is under question (Copeland, 1947; Holttum, 1949), multicellular hairs have appeared in two species. On the prothallus of *L. parksii* Copel. two-celled marginal hairs appeared sparingly at nine months; when two to six years old several two- or three-celled hairs could always be found towards the tip of a lobe or branch of the thallus usually on the margin (*Fig. 17*) but also on the surface. The same type of two-celled hair appeared sparingly. on *L. avenia* Presl at 13 months.

In the Grammitidaceae some species have a heavy growth of branched hairs with an occasional two-celled hair along the margin (Stokey & Atkinson, 1958). Some of the hairs have a slender spine-like branch, as in *Xiphopteris delitescens* (Maxon) Copel. (*Fig. 27*), or even two such branches as in *Ctenopteris jubiformis* (Klf.) J. Smith (*Fig. 28*); or all branches may have a glandular cell at the tip as in *C. suspensa* (L.) Copel. (*Fig. 29*). The hairs of the Grammitidaceae differ from those of the Polypodiaceae *s.s.* in arising regularly on the margin rather than on the surface.

The significance of multicellular and branched hairs on the fern gametophyte can hardly be considered apart from the larger question which would include the distribution and type of unicellular hairs. We need much more information about the occurrence and distribution of all types of hairs on both young and old gametophytes.

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Progress in the Study of Dryopteris Hybrids

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In the course of searching for *Dryopteris* hybrids to send to Dr. Stanley Walker for the cytotaxonomic studies recently reported in this JOURNAL,[1] I felt a need for a diagram bringing out their inter-relationships. Now that data as to chromosome numbers can be added, it has seemed worth while to publish such a diagram. Before it can be presented, however, some considera-

[1] This JOURNAL *49:* 104–112. 1959.
[2] International Code of Botanical Nomenclature, Art. H 1. 1956.